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DOES NEOTENY OCCUR IN HOLARCTIC LAMPREYS (PETROMYZONTIDAE)?

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ABSTRACT

The occurrence of neoteny in Petromyzontidae has been mentioned in the literature. Zanandrea (1956, 1957, 1958, 1961) reported neoteny in ammocoetes of Lampetra zanandreai. Hubbs (1971), as well as Walsh and Burr (1981), described it in metamorphosed specimens of Entosphenus lethophagus and Lampetra aepyptera, respectively. However, the above authors did not give sufficient evidence supporting the existence of neoteny in lampreys.

RÉSUMÉ

La littérature mentionne le phénomène de néoténie chez les Pétromyzontidae. Zanandrea (1956, 1957, 1958, 1961) a rapporté la néoténie chez les ammocoètes de Lampetra zanandreai. Pour ce qui est des spécimens métamorphosés, Hubbs (1971) l'a décrite pour l'espèce Entosphenus lethophagus ensuite, Walsh et Burr (1981) l'ont décrites pour Lampetra aepyptera. Néanmoins, les articles des auteurs précités manquaient de preuves convainquantes quant à l'existence de la néoténie chez les lamproies.

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INTRODUCTION

The general biology of the Holarctic lampreys (Petromyzontidae) is relatively well-known. However, the details of their reproduction and especially the phylogenetic relation between parasitic and nonparasitic species is in need of additional observation. After studying all 36 species of Petromyzontidae (Vladykov and Kott 1979A), I conclude that, due to the extreme complexity of the lamprey reproductive cycle, the authors who claimed to observe cases of neoteny among lampreys did not give sufficient proof. The purpose of the present article is to analyze objectively their arguments about the occurrence of neoteny among lampreys.

DEFINITION OF NEOTENY

Zanandrea (1956, p.426) was the first author who claimed to find a case of "complete neoteny" in lampreys, namely, in the nonparasitic northern Italian species, Lampetra zanandreai. In three subsequent papers published in 1957, 1958, and 1961 he repeated the same statement. In an article of 1957 he stated, that on March 18, 1955, he collected ammocoetes of which "twelve showed well-developed ovaries containing eggs which were macroscopically visible on dissection and obviously in an advanced state of maturity... One larva showed well-developed principal secondary characters, namely, enlargement of the two dorsal fins and fusion of these fins, development of the anal pseudofin, and transparent body wall through which the eggs could be seen. Such characters are normally only associated with adults which are about to spawn. The neotenic specimens, which were all females, were collected during the spawning season". Unfortunately, he did not give the definition of the term "neoteny".

No doubt, Zanandrea was familiar with the following authors: Kollman (1883)[1], who was the first to propose the term "neoteny"; Wolcott (1940); deBeer (1951); and Gallien (1952) to mention a few, although he did not include them in his bibliography.

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[1] The paper by Kollman was not available to me. Hence, I was unable to determine the exact date of publication which according to deBeer (1951) is 1883, and according to Gould (1977) is 1885.

In my opinion, a definition of neoteny and related terms was clearly given by deBeer (1951, p. 52): "In principle, paedogenesis and progĕnĕse apply to cases where the larva becomes precociously sexually mature; neoteny to cases where the adult animal retains larval characters. But as there are no hard and fast distinctions between them, they are all included here under neoteny." The neoteny was observed in a number of animal groups, both invertebrates and vertebrates (deBeer 1951; Gould 1977).

Recently, several publications appeared with a discussion of which term is more useful: neoteny or paedogenesis. Pierce and Smith (1979, 1980) favour the term neoteny, while Sullivan (1980) and Wake (1980) prefer paedogenesis.

Pierce and Smith (1980) made the following remark about the importance of the above discussions: "Debate over terminology may often appear to be a trivial exercise, but a common terminology serves as the basis for communication between scientists. When there exists no consensus or uniformity in the use of important terms, it becomes impossible to convey ideas and findings clearly, and scientific progress may be seriously impeded. An acute lack of such consensus occurs in the use of several terms describing larval reproduction (e.g., paedogenesis, paedomorphosis, neoteny and progenesis)".

As a typical case of neoteny, one must mention Ambystoma mexicanum. Completely metamorphosed individuals, which are rather rare in nature, are terrestrial in habit. Unmetamorphosed axolotls are aquatic in habit and possess three pairs of external gills and a high flat tail. In spite of the larval appearance, they are sexually mature and reproduce profusely. According to Gallien (1952, p. 72), this is a case of "nĕotĕnie facultative et totale".

Some other urodele amphibia, such as Necturus and Proteus, retain juvenile characteristics, reproduce and live permanently in water without metamorphosing into the adult stage. Gallien (1952, p. 71) considers this case as "nĕotĕnie totale et obligatoire".

External appearance of larvae and adults of Urodeles is very similar, which is not the case in Petromyzontidae.

THE LIFE-CYCLE OF PETROMYZONTIDAE

In lampreys, there are two very distinct stages in the life-cycle: (a) the ammocoete or larval stage, and (b) the adult or metamorphosed stage. The external appearance of ammocoetes is characterized by eyes hidden under the skin, by the presence of an oral hood instead of a sucking disc at the anterior end of the body (Figure 1), and by the absence of a urogenital papilla. The nutritive and respiratory water current enters through the mouth, which is guarded by a ring of oral cirri, and exits through the seven gill slits. Most of the time, the ammocoete lies concealed in the silt deposits of rivers and streams (Hardisty and Potter 1971A). Ammocoetes have a longer life span than the adults.

The metamorphosed individuals, instead of an oral hood, have now a sucking disc provided with teeth, and a urogenital papilla which is longer in males than in females. All lampreys belong to one of two biotypes: parasitic or nonparasitic. The parasitic species retain a functional intestinal tract following metamorphosis and feed intensively on the blood of fishes or cetaceans prior to reaching sexual maturity. The nonparasitic species do not retain a functional intestinal tract following metamorphosis and therefore cannot feed. For interrelations between parasitic (stem) and nonparasitic (satellite) species of lampreys, consult Vladykov and Kott (1979B). Individuals of both types of lampreys reproduce only once and die shortly after spawning.

At the onset of metamorphosis, ammocoetes of nonparasitic species are longer than those of parasitic species.

There is an agreement among authors (Hubbs and Trautman 1937; Hubbs and Potter 1971; Hardisty and Potter 1971B; Vladykov and Kott 1979B) that most probably the nonparasitic species are derived from parasitic species. This is a striking feature of lamprey phylogeny, unique among vertebrates, involving the repetitive trend towards the elimination of feeding in the metamorphosed stage. This trend can be visualized as follows: in a formerly parasitic species the duration of the ammocoete stage is extended, permitting a longer feeding period which allows a considerable development of gonads previous to metamorphosis into the adult stage.

As an illustration of the time required for the different life stages in a nonparasitic lamprey, such as Ichthyomyzon fossor, see Leach (1940).

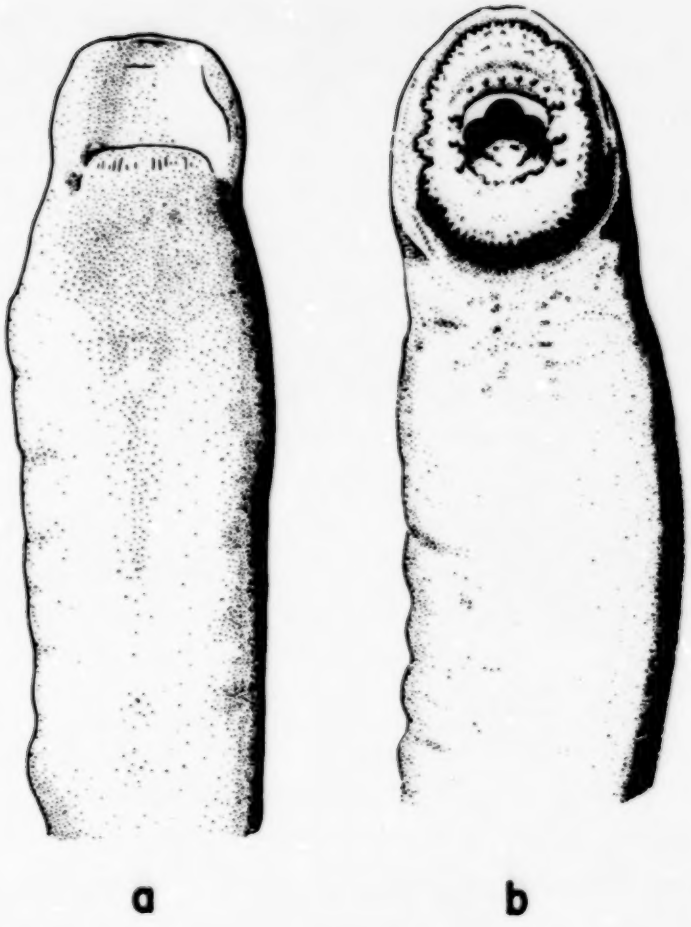

FIGURE 1: External changes in the head region of Lenthenteron wilderi during metamorphosis (from Vladykov 1949): a - ammocoete, b - adult lamprey.

The well-developed eggs in ammocoetes were observed in several nonparasitic species: Ichthyomyzon fossor (Leach 1940; Vladykov and Kott 1979B), Lampetra zanandreai (Zanandrea 1956), Lampetra planeri (Hardisty and Potter 1971A), and Lethenteron wilderi[2] (Vladykov and Kott 1979B). No doubt, in ammocoetes of all nonparasitic species, the same situation exists.

The reproductive process in Urodeles is simple, without body contact. In lampreys, the spawning act is very complex and elaborate (Hardisty and Potter 1971B). After a nest on the bottom of the stream is constructed, the female is attached to a stone near the leading edge of the nest. In the spawning act, the male slides along the dorsolateral surface of the female. With the anterior regions of their trunks more or less parallel, the male then curls the posterior section of the body in a tight right-handed spiral round the female. The tail of the male is then moved backwards until the cloacal regions of both sexes are in close proximity. The urogenital papilla, which is longer in males, helps to direct the sperm towards the extruded eggs. Sterba (1962) gives a good illustration (Figure 2) of the pairing act in Lampetra fluviatilis.

To summarize briefly, a successful reproductive act in both nonparasitic and parasitic lampreys requires the following conditions: ammocoetes should have mature gonads, and metamorphosed specimens, in addition to a urogenital papilla, should possess a sucking disc enabling the female to anchor herself to the bottom of the stream and the male to attach to the female.

The ammocoetes of Lampetra zanandreai described by Zanandrea (1956) as neotenic are typical larvae, which are far from being considered spawning specimens. They still lack the sucking disc and urogenital papilla.

A presence of rather well-developed gonads in ammocoetes of nonparasitic lampreys close to the onset of metamorphosis is usually regarded by authors as a normal phenomenon. According to observations by Leach (1940), an important difference exists between parasitic and nonparasitic lampreys, namely, there is a tendency towards precocious sexual maturity in the latter, in which there is no growth phase interpolated between metamorphosis and the assumption of full sexual maturity. No doubt, Zanandrea (1956) was acquainted with

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[2] For the explanation of the term Lethenteron wilderi, consult Vladykov and Kott (1982).

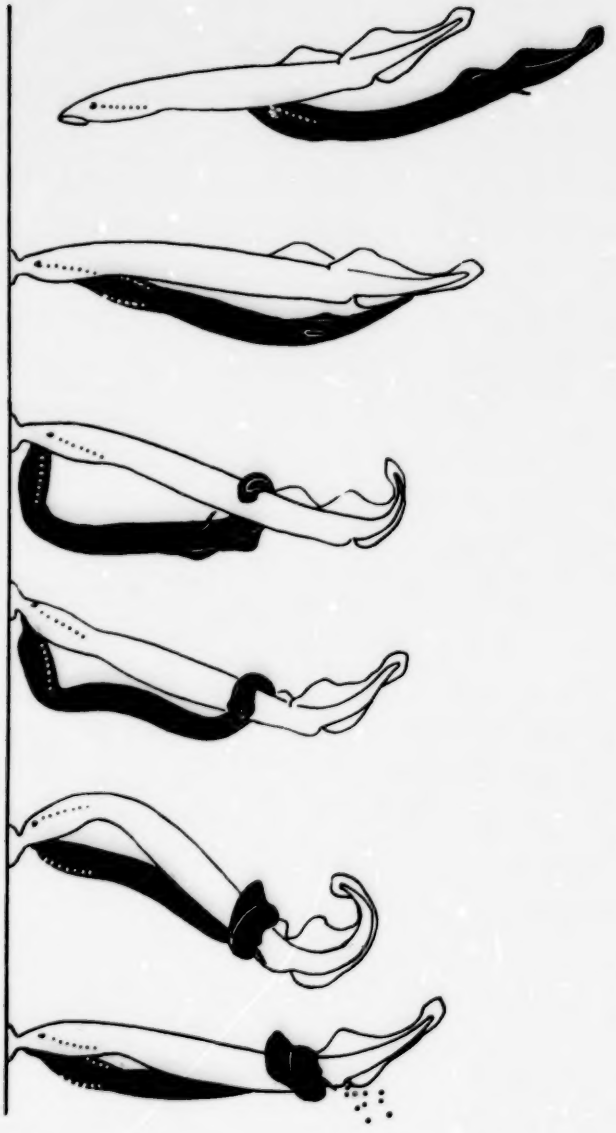

FIGURE 2: The pairing act in Lampetra fluviatilis (from Sterba 1962). Male (solid black) has a relatively long urogenital papilla, but lacks the anal fin fold. Female (black outline) has an anal fin fold well developed, but its small urogenital papilla is not shown.

Figure 2 from: Sterba, G. 1962. Die Neunaugen (Petromyzonidae). In Handbuch der Binnenfischerei Miteleuropas. Vol. 3. Edited by R. Demoll and H.N. Maier. Permission to reproduce the figure was granted by E. Schweizerbart'sche Verlagebuchhandlung.

important studies on Ichthyomyzon fossor by Leach (1940). Nevertheless, he considered a presence of developed eggs in ammocoetes of L. zanandreai as a case of neoteny.

Hubbs (1971) claimed to observe a case of neoteny in Entosphenus lethophagus, a nonparasitic species from the western coast of North America. To support the correctness of his observations, he presented a photograph (Figures 1, 2) of metamorphosed specimens of E. lethophagus in different stages of maturation. Spawning male and female ("nuptial" specimens) he considered as neotenic. However, his photograph clearly shows normal mature specimens of E. lethophagus, which retain no obvious larval characteristics and, therefore, cannot be considered neotenic.

Recently, Walsh and Burr (1981) claimed to have observed the presence of neotenic conditions in Lampetra aepyptera. They presented photographs (Figure 5) of four metamorphosed specimens, two of which (A and C), collected in 1977, are a "fully nuptial" male and female, which are not considered neotenic by the authors. The two others (B and D) obtained in 1980, are regarded by them as a "partially neotenic" male and a "partially neotenic" female.

Since temperatures in Terrapin Creek are similar to those of other streams that contain normal adults (nuptial specimens) of L. aepyptera, unusual temperatures were ruled out by the authors as a factor suppressing nuptial development.

Concerning the "partial neoteny" of specimens of L. aepyptera from Terrapin Creek (B and D), the authors make the following erroneous statement: "the failure...to exhibit normal secondary sexual characters is tentatively attributed to limited food during the ammocoete stage". Limited food in the water could affect the total length of metamorphosed ammocoetes, but not the development of secondary sexual characteristics. Indeed, according to precise observations by Leach (1940, p. 30), an ammocoete of I. fossor, "kept in a pure washed sand for almost 2 years", metamorphosed into a normal sexually mature female containing 780 eggs approximately 1.2 mm in diameter. This female measured only 92 mm in contrast to the average size of 112-122 mm.

The 92 mm female of I. fossor corresponds to a "partially neotenic" female of L. aepyptera, 114.8 mm in length, from Terrapin Creek, about which Walsh and Burr (1981, Figure 5 B) stated that its "coelom is packed with mature ova".

CONCLUSION

In conclusion, I must summarize my objections to authors who described the existence of neoteny in Petromyzontidae.

1. Zanandrea (1956) claimed to find neotenous ammocoetes of Lampetra zanandreai. His conviction is mainly based on well-developed ovaries in 12 ammocoetes, containing eggs which were macroscopically visible on dissection and obviously in advanced state of maturity. However, developed eggs in premetamorphic ammocoetes were observed by several authors in other species of nonparasitic lamprey. In addition, one of Zanandrea's ammocoetes had two dorsal fins close together and the "anal pseudofin" had started to develop. Zanandrea did not give any proof that his neotenic ammocoetes would be metamorphosed into neotenic adults. In reality, there is no available description of the "adult neotenic" lamprey. There is a clear distinction between ammocoetes with developed eggs and sexually mature individuals. It should be added also, that Zanandrea had no neotenic ammocoetes of the male sex.
2. In the case of metamorphosed specimens of Entosphenus lethophagus (Hubbs 1971) and Lampetra aepyptera (Walsh and Burr 1981) the above authors, to support the correctness of their observations, presented photographs of both species in different stages of maturation. However, the photographs clearly show normal mature specimens, which retain no obvious larval characteristics and therefore cannot be considered neotenic.

In conclusion, on the basis of facts presented here, my answer to the title question is negative: neoteny does not occur in Petromyzontidae.

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